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AGRICULTURAL MEMORANDUM NO. 656

On some temperature dependent physiological processes in organisms that tend to take up the temperature of their surroundings

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1. INTRODUCTION

By deliberate choice, most of the work at Meteorological Cambridge has been concerned with problem solving; there has generally been a definite end point in view. By contrast, this note arises out of scientific curiosity. That is not to say that there will be no applications, but the immediate concern is to move from a particular example in one area (onion storage) to some general conclusions, and then possibly to apply these conclusions to a completely different area.

It is apparent that an understanding of the reasons for the wide range of response of stored onions to accumulations of onion bulk temperature may not be easy to achieve. The view was taken in Ag Mem 361 that the observed spread of results might be attributed to varying efficiencies of sprout suppressant procedures. Whilst the evidence may point that way, it could obscure the need to look beyond the field and storage data to some of the more fundamental relationships between crop physiological response and temperature. Many conclusions concerning plants, whose temperatures are somewhat plastic, responding to the ambient environment, would presumably be equally valid for other organisms which tend to take up the temperature of their surroundings.

At some stage, models of growth and development may be seen as preliminary requisites for comment and advice. Temperature effects must obviously be included and it is important to realise that responses to temperature and temperature change may not be simple and that there are a wide variety of options: each option may imply a different dominant physical or chemical process.

2. THE DOMINANT REACTION

We define Q_{10} as the ratio of the rates of a process at successive (increasing) temperatures $10^{\circ}C$ apart. In the notation of Ag Mem 622

$$Q_{10} = \frac{K_{10}}{K_0}$$

where K_{10} = reaction rate at $10^{\circ}C$

K_0 = reaction rate at $0^{\circ}C$

The observation that onions may be held in store with little sprouting at both low temperatures ($0^{\circ}C$) and high temperatures ($30^{\circ}C$), whilst a significant increase in sprouting occurs at intermediate temperatures, would seem to suggest that 2 distinct constraints apply at the 2 extremes of temperature.

An extension from this particular observation to the general case might imply that

the complex organisms of interest to us, when subjected to a variety of environmental inputs, undergo a variety of internal physical processes and chemical reactions which interact, may show a mutual dependence and which, not uncommonly, may provide mutual constraints. The net effect of these interacting physical and chemical processes determines the rate of growth and development, and even the morphology of the organism.

A high correlation between rates of growth and development, and temperature accumulations would be expected whilst strongly temperature dependent processes dominate the net result. The strongest associations might be expected at low temperatures, since the linear temperature dependence that is not uncommonly observed for plant physiological processes implies that, as the temperature increases, Q_{10} (for the dominant process) decreases. On such considerations we should expect temperature accumulations to accord better with early growth changes in spring, rather than with later crop response in high summer and towards harvest.

When the net growth or development is constrained by processes with a low Q_{10} value, for example by photo-chemical reactions or by diffusion or mass-flow processes, no clear association with environmental temperature might be expected. At average environmental temperatures sufficiently high to permit of high rates of enzyme (ie chemical) reactions, limits to growth would then be imposed by other (ie primarily physical) processes.

3. THE COMBINATION OF REACTION RATES

In the case of onions at low temperature, the reaction rate K_0 of the initial controlling process is seen as low, though Q_{10} is not necessarily low. At high temperatures, the reaction rate of this first reaction increases from K_0 to K_{30} but, at the same time, control of the net production (manifest as sprouting) passes to a second process, which may be indifferent to temperature level.

It would seem that the temperature relationship of metabolic processes should not be regarded as fixed. In addition, we should not expect individual processes to proceed in isolation in the organism.

Our interest is seen to lie in:-

(a) the temperature response of the individual process
(b) the net effect when 2 or more effectively independent processes are involved at a given stage of growth.

Net effects might be expected to show:-

(c) which of concomitant (or sequential) process rates are limiting
(d) the sense of the processes, ie whether they act in concert towards a common goal or whether they conflict or compete for common resources.

Whilst real analogues are not actively sought in the remainder of this paper for the alternative methods of combining reaction or process rates, examples which readily spring to mind under (d) above are:-

- the consumption of photosynthates in respiration
- the competition between root and shoot growth for photosynthates.

Some simple options for the combination of process rates are provided when:-

(i) the smaller of the 2 process rates is regarded as limiting and as the net process rate for their combined effect

(ii) the net effect is regarded as being given by the difference between 2 process rates

(iii) the net effect is regarded as being given by the product of 2 process rates.

A study of net process rates is not our end point. Our interest ultimately lies in those changes in the organisms that we can see, weigh or measure; that is, in the metabolic change accumulated in a finite time interval and in the time integral

$$\int_0^t K_T dt$$

Two further options should be considered here:

(i) the metabolic change is simply a function of K_T; the accumulated metabolic change will commonly be a linear function of time

(ii) the metabolic change over some time interval is a function both of K_T and the total metabolic change (from some zero) up to the commencement of the time interval; the accumulated metabolic change will now commonly be an exponential function of time.

4. THE INDIVIDUAL REACTION RATE AS A FUNCTION OF TEMPERATURE

We consider the following simple alternatives

(A) K_T constant with temperature

(B) K_T a linear (increasing) function of temperature

(C) K_T a linear (decreasing) function of temperature

(D) K_T a parabolic function of temperature

(E) K_T an exponential function of temperature

These are shown schematically in Figure 1.

Case A

$$K_T = \text{constant}$$

$$Q_{10} = \frac{K_T}{K_{T-10}} = 1$$

(i) $$A_t = \int_0^t \frac{dA_t}{dt}.dt \qquad \text{and} \qquad \frac{dA_t}{dt} = K_T$$

Integrating: $$\boxed{A_t = K_T.t = K_0.t}$$

(ii) $\frac{dA_t}{dt} = K_T \cdot A_t \qquad \frac{dA_t}{A_t} = K_T \cdot dt$

Integrating: $\log A_t = K_T t + \text{constant}$

and $\boxed{A_t = e^{K_0 t} - 1}$ since $K_T = K_0$

Case B

$$K_T = K_{T-10} + m.\left[T - (T-10)\right]$$

$$K_T = K_{T-10} + 10m = K_{T-10} + \text{constant}$$

As T increases, Q_{10} decreases and $Q_{10} = \phi\left[1/T\right]$

(i) $$A_t = \int_0^t K_T dt$$

Obvious diurnal variations of temperature could be introduced at this stage. We consider here simply the case where temperature increases uniformly with time from a base of T_0 to a temperature T, in the time interval 0 to t.

$$A_t = \int_0^t \left[K_0 + m.(T-T_0)\right] dt$$

$$A_t = \int_{T_0}^T \left[K_0 + m.(T-T_0)\right] \frac{dt}{dT}.dT$$

$$A_t = \frac{t}{T-T_0} \int_{T_0}^T \left[K + m.(T-T_0)\right] dT$$

$$A_t = \frac{t}{T-T_0}\left[m\frac{T^2}{2} + T(K_0 - m.T_0) \right]_{T_0}^T$$

and $\boxed{A_t = K_0 t + \frac{m}{2}.(T-T_0).t}$

(ii) $$\frac{dA_t}{dt} = K_T \cdot A_t$$

(ii) $\frac{dA_t}{dt} = K_T \cdot A_t$ and $A_t = e^{K_T \cdot t} - 1$ as before

Hence $$\boxed{A_t = e^{K_0 \cdot t} \cdot e^{b(T-T_0) \cdot t} \cdot e^{a(T-T_0)^2 \cdot t} - 1}$$

Case E

Here K_T is represented by $K_T = K_0 \cdot e^{a(T-T_0)}$

(i)

$$A_t = \int_0^t K_T dt$$

If temperature rises steadily from T_0 to T over the time interval 0 to t

$$\boxed{A_t = \frac{K_0}{a} \cdot \frac{t}{(T-T_0)} \cdot \left[e^{a(T-T_0)} - 1 \right]}$$

(ii)

$$\frac{dA_t}{dt} = K_T \cdot A_t$$

and $A_t = e^{K_T \cdot t} - 1$ as before

$$A_t = e^{K_0 \cdot e^{a(T-T_0)} \cdot t} - 1$$

$$\boxed{A_t = \left[e^{K_0 t} \right]^{e^{a(T-T_0)}} - 1}$$

5. THE COMBINED REACTION RATES OF 2 PROCESSES AS A FUNCTION OF TEMPERATURE

5.1 We consider first the situation where the smaller reaction rate determines the net effect. Some alternatives are shown schematically in Figure 2 for the case where temperature increases uniformly with time. Attention is now drawn to the fact that Q_{10} and, more importantly, A_t will show a discontinuity at the temperatures where the rate curves K_T intersect.

5.2 The situation where the net effect is determined by the difference between the 2 process rates is shown schematically in Figure 3. If the rate of

As before, we may infer

$$A_t = e^{K_T \cdot t} - 1$$

and with

$$K_T = K_0 + m(T-T_0)$$

$$\boxed{A_t = e^{K_0 \cdot t} \cdot e^{m(T-T_0)t} - 1}$$

Case C

Here $K_T = K_{T-10} - m\left[T - (T-10)\right]$

and the diagrams in Figure 1 may be obtained by considerations of symmetry.

Case D

Here K_T is seen as a parabolic function of temperature and described by a rate of change of K_T which increases (or decreases) uniformly with temperature.

That is $\dfrac{\partial K_T}{\partial T} = mT + \text{constant}$

and generally

$$K_T = a(T-T_0)^2 + b(T-T_0) + K_0$$

(i) $$A_t = \int_0^t K_T dt$$

If temperature rises steadily from T_0 to a value of T over the time interval 0 to t:

$$A_t = \frac{t}{T-T_0}\left[\frac{a(T-T_0)^3}{3} + \frac{b(T-T_0)^2}{2} + K_0(T-T_0)\right]_{T_0}^{T}$$

$$\boxed{A_t = \left[K_0 + \frac{b}{2}\cdot(T-T_0) + \frac{a}{3}\cdot(T-T_0)^2\right]t}$$

production of some material is designated by the first of the 2 process rates considered and its rate of removal by the second process rate, then when the second exceeds the first A_t will be zero.

5.3 The situation where the net effect is determined by the product of the 2 process rates is shown schematically in Figure 4.

6. APPLICATION

Epstein and Thomson (1974) report on nematode mutants which emerge paralysed on incubation at temperatures of 20°C or above. The normal larvae develop without mishap at any temperature between 15°C and 25°C. Differences in muscle structure can be shown between the normal and mutant nematodes on incubation at temperatures higher than 20°C.

The explanation offered is that the chemical composition of an enzyme which acts during the assembly of muscle is slightly different in the 2 cases; in the mutant the enzyme is unstable above 20°C.

Alternative explanations can be offered on the basis of this note.

If we postulate that 2 (or more) independent processes are involved in the production of the components that are brought together to form normal muscle tissue and that the rate of organisation of normal muscle is determined by the smaller production rate of the 2 (or more) essential constituents, then the situation is that shown schematically in Figure 2.

Any temperature at which the 2 rate curves, K, intersect is necessarily associated with a discontinuity in A_t, the rate of accumulation of the product to which the 2 processes contribute.

For the mutant nematodes, we have only to postulate that such an intersection (and discontinuity) occurs at around 20°C. (By implication, such discontinuities could also occur for "normal" nematodes if incubated at temperatures outside the range normally encountered.)

To shift the point of discontinuity, we do not necessarily have to postulate any change in the variation of the 2 process rate curves with temperature but merely some slight difference in one of the process rates at some low (base) temperature, ie some slight shift of origin.

Such a concomitant requirement for an "abnormal" gene is possibly a less radical option than that the muscle building enzyme should have a different chemical composition in the normal and mutant species.

7. COMMENT

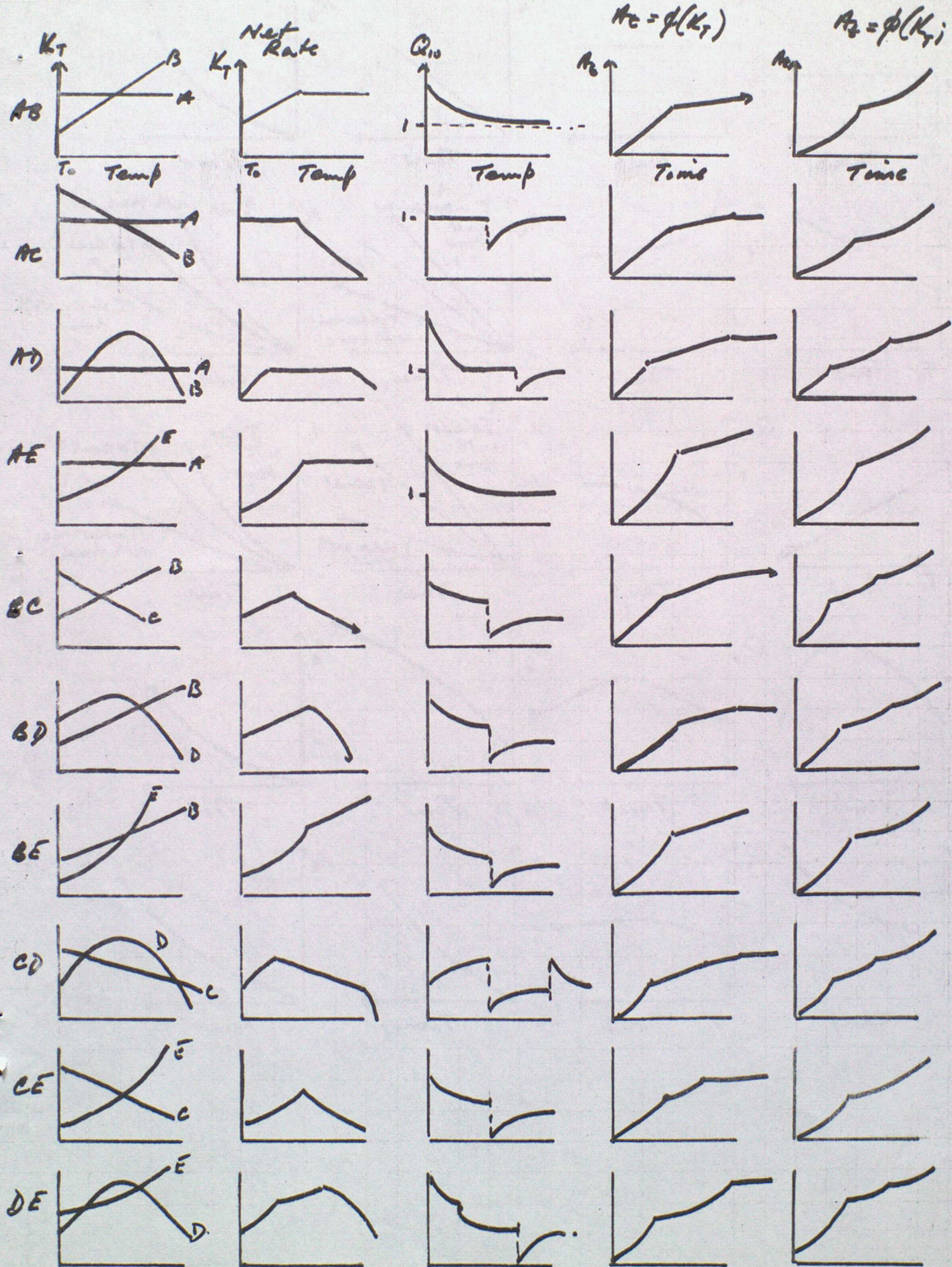
If we deal in process rates and not necessarily with detailed nature of the process, ie physical, chemical, biochemical, economic, then much of what has been discussed is valid for a wide variety of systems that respond to impressed events.

Meteorological Office
Cambridge
August 1974

Reference

Epstein, H
Thomson, J N
1974
Dystrophies; Inborn Abnormality in Muscles
Nature August 16 (250, 57; 1974)
Report in The Times, August 16, 1974.

FIGURE 2 — COMBINED PROCESS RATES (SMALLER LIMITING).



INDIVIDUAL PROCESS RATES

FIGURE 1

$A_c = \phi(K_T)$ $\quad A_c = \phi(K_T; A_c)$

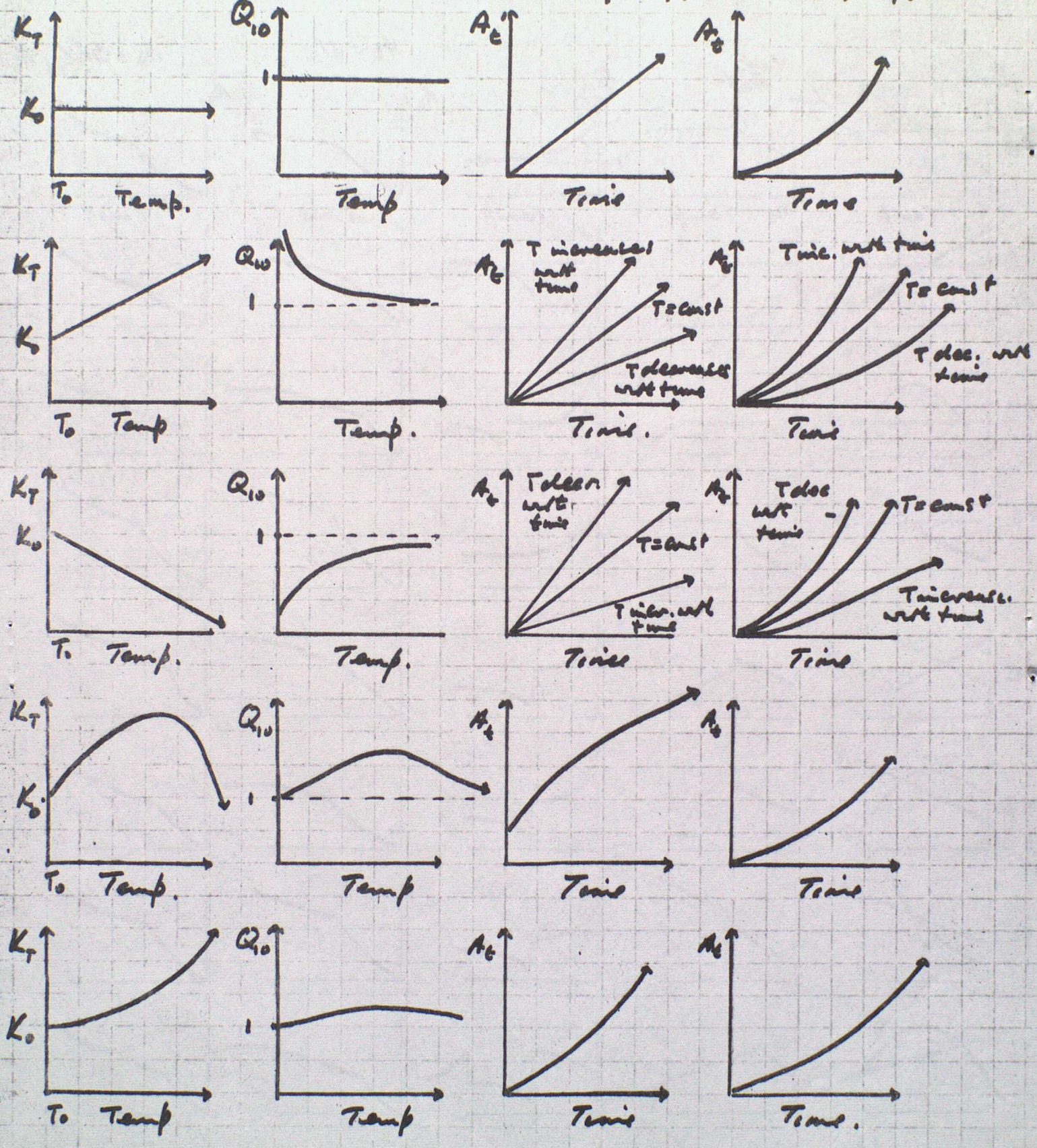


FIGURE 4 — COMBINED PROCESS RATES (PRODUCT)

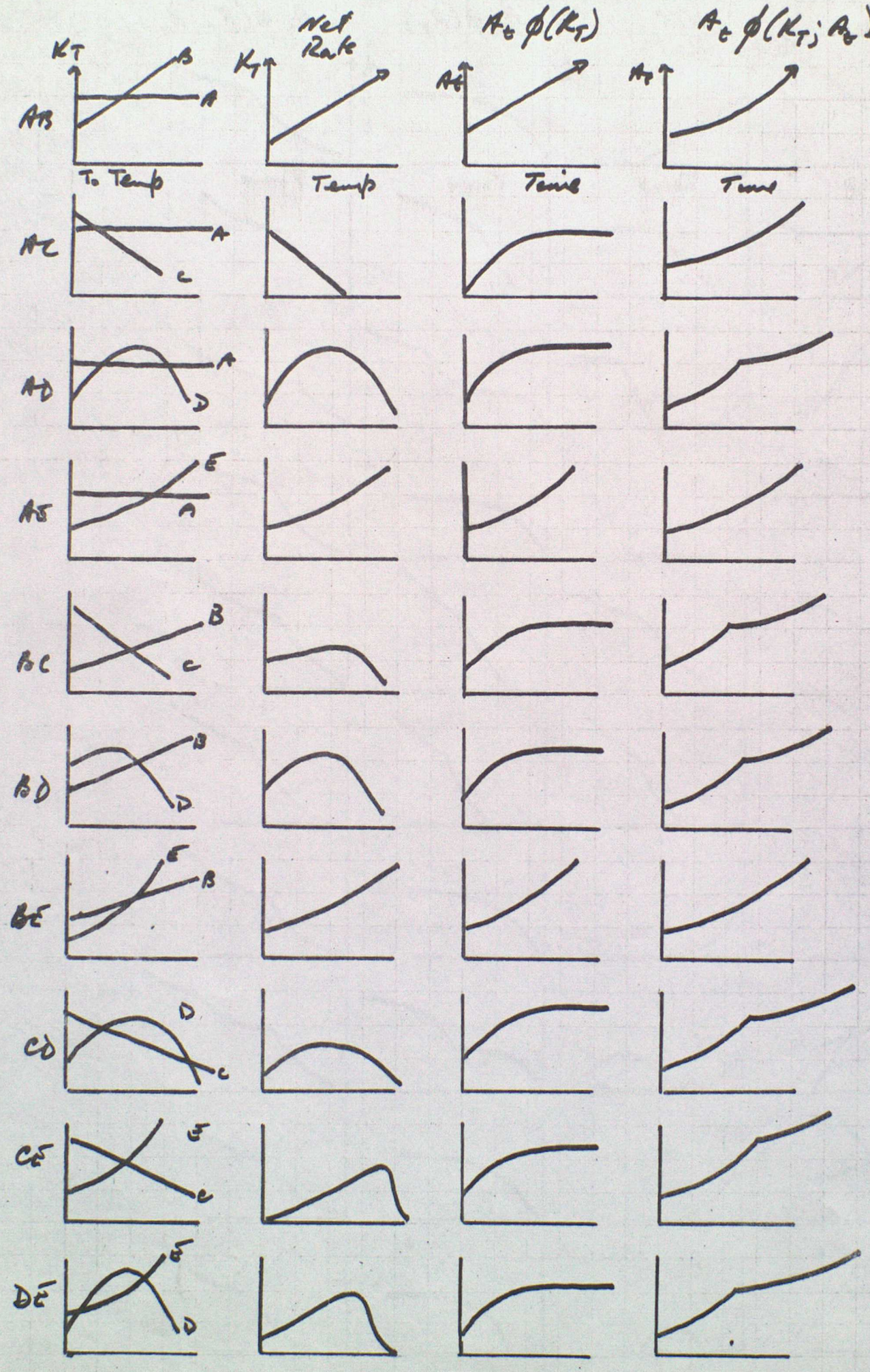


FIGURE 3 — COMBINED PROCESS RATES (DIFFERENCES)